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Dedication: Arnel R. Hallauer, Scientist, Maize Breeder, Quantitative Geneticist

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Abstract

Arnel R. Hallauer has dedicated his life to breeding; therefore, it is appropriate that this issue of Plant Breeding Reviews be dedicated to him. Dr. Hallauer's primary contributions have been in understanding quantitative inheritance in maize, developing breeding methodology, evaluating and utilizing recurrent selection for population improvement, and developing inbred lines for use in maize hybrids. Dr. Hallauer has also been very involved in graduate student education. The success of is students in academia and industry is a measure of his ability as a graduate educator and represents one of his greatest contributions to plant breeding. He has also been extensively involved in international activities and is known throughout the world for the impact of is efforts in that arena. Sprague and Lamkey (1992) have reviewed Dr. Hallauer's career in the context of the development of quantitative genetics and his research career will be emphasized here.

Disciplines

Agricultural Science | Agronomy and Crop Sciences | Plant Breeding and Genetics

Comments

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Dedication: Arnel R. Hallauer Scientist, Maize Breeder, Quantitative Geneticist*

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Arnel R. Hallauer has dedicated his life to breeding; therefore, it is appropriate that this issue of *Plant Breeding Reviews* be dedicated to him. Dr. Hallauer's primary contributions have been in understanding quantitative inheritance in maize, developing breeding methodology, evaluating and utilizing recurrent selection for population improvement, and developing inbred lines for use in maize hybrids. Dr. Hallauer has also been very involved in graduate student education. The success of his students in academia and industry is a measure of his ability as a graduate educator and represents one of his greatest contributions to plant breeding. He has also been extensively involved in international activities and is known throughout the world for the impact of his efforts in that arena. Sprague and Lamkey (1992) have reviewed Dr. Hallauer's career in the

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BIOGRAPHICAL SKETCH

Arnel Roy Hallauer was born on May 4, 1932, at Netawaka, Kansas. His interest in maize research began in the fall of 1946, when at age 14 he had a part-time job with Dr. Lloyd A. Tatum harvesting experimental maize trials in northeast Kansas. He continued working part time with Dr. Tatum while attending high school (1946–1950), planting experimental maize trials in the spring and harvesting them in the fall. During the summer months of his high school years, he detasseled maize for the production of double-cross hybrid seed for Mr. Carl Overly of the Kansas Crop Improvement Association. These associations with Dr. Tatum and Mr. Overly led him to Kansas State University where he received his B.S. degree with honors in 1954 with a major in plant science. During his undergraduate studies, he was continuously employed part time with the cooperative federal-state maize-breeding project directed by Dr. Tatum at Kansas State University. There he experienced all aspects of the breeding project including preparing seed, planting, collecting data, harvesting, pollinating in the breeding nurseries, and analyzing and summarizing data of experimental trials.

After finishing his undergraduate degree, Arnel served for two years in the military (1954–1956). Dr. Tatum, impressed with his young assistant's dedication and work ethic, urged Arnel to attend graduate school for an advanced degree in plant breeding. After considering offers from many universities, he chose Iowa State because the offer included the opportunity to work with Dr. George F. Sprague, a maize breeder and geneticist who had a highly-regarded research program. Dr. Hallauer completed the requirements for the M.S. degree in plant breeding in 1958. While working for the USDA-ARS, he continued in graduate school and received his Ph.D. in 1960. Dr. W. A. Russell served as his major advisor for the Ph.D. degree after Dr. Sprague was transferred to Beltsville, Maryland, in 1958 to become the USDA-ARS Investigations Leader for maize and sorghum research.

With the completion of his graduate training, Dr. Hallauer was transferred to North Carolina State College as a USDA-ARS postdoctoral research geneticist to spend a year with Professors H. C. Robinson and R. H. Moll. In 1962, he was transferred back to Ames as a USDA-ARS research geneticist; he continued in this capacity until 1989. In December of 1989, Dr. Hallauer retired from the USDA-ARS and accepted a position with Iowa State University as professor of plant breeding. In 1991, he was named the C. F. Curtiss Distinguished Professor in Agriculture.

QUANTITATIVE GENETICS

Dr. Hallauer has devoted his career to understanding the inheritance of agronomic traits in maize. Because most traits of importance in maize are controlled by many genes, Dr. Hallauer was mainly interested in the quantitative genetics of maize populations. The main questions of interest were the types of gene action controlling quantitative traits, the amounts and types of genetic variance in maize populations (additive, dominance, or epistatic), and the heritability of agronomic traits. These questions were of utmost importance because they were directly related to the rate of genetic gain that could be expected from recurrent selection in maize populations.

Dr. Hallauer began his career studying the inheritance of grain moisture at harvest and time of flowering in maize. He then focused his attention on estimating the genetic variance components for agronomic traits in open-pollinated populations and synthetic cultivars of maize. He found that additive genetic variance frequently accounted for the majority of the total genetic variation for grain yield, and dominance variance, although much smaller, was usually significant and accounted for the remainder. Extensive studies to detect epistatic genetic variance in maize synthetics revealed that it was a minor contributor to the total genetic variance for grain yield.

The one major exception to the pattern of genetic variances observed by Dr. Hallauer was Iowa Stiff Stalk Synthetic (BSSS). Variance component studies in BSSS have consistently shown that the additive and dominance variance components are equal in magnitude. This result was in direct contrast to average results from other maize populations where the additive variance was usually twice the dominance variance (Hallauer and Miranda 1988). This result must be directly related to the choice of inbred lines used to form BSSS. It is also interesting to note that BSSS is one of the most important sources of inbred lines in the maize industry.

One of the most striking phenotypic observations in maize is the extensive inbreeding depression that is observed for grain yield when maize is self-pollinated. The studies that Dr. Hallauer conducted on inbreeding depression in maize were among the first and are now classics (Hallauer and Sears 1975; Good and Hallauer 1977). These studies demonstrated that inbreeding depression for grain yield was a linear function of the inbreeding coefficient. Linear regression usually accounted for 93 to 99% of the variation among means of the inbred generations. The linearity of inbreeding depression was additional evidence in support of conclusions from the variance component studies that epistasis was not important in maize synthetics.

Because of the importance of directional dominance in maize as evidenced by the inbreeding depression observed for grain yield, there has been extensive research into tester theory and the relationship between line and hybrid performance. The choice of testers in a maize improvement program is one of the more important decisions a breeder makes in a breeding program. The choice of a tester is highly dependent on the level of dominance (partial to complete dominance vs. overdominance) and the frequency of favorable alleles in the tester population (or line) in comparison to the population being tested. The theory shows that testers with a low frequency of favorable alleles will maximize genetic variance among testcross progenies for all levels of dominance. The problem is that maize breeders are reluctant to use low-yielding inbreds as testers and inbreds that are low yielding may not necessarily have low frequencies of alleles for grain yield. Hallauer and Lopez-Perez (1979) conducted an extensive study evaluating the discriminatory power of five types of testers selected for their expected differences in allelic frequency for grain yield. The five testers were crossed to 50 S_1 lines and the 50 S_8 lines derived from these S_1 lines. Four of the testers were related to the population the lines were derived from and one of the testers was unrelated. Hallauer and Lopez-Perez found that genetic variance among testcrosses ranked according to the expected frequency of the favorable allele for grain yield. Genetic variances among testcrosses to the unrelated tester were similar to those found with the lowest yielding (and lowest expected frequency of the favorable allele) tester. These results were a significant finding because they demonstrated that unrelated testers (usually from the opposite heterotic group) have discriminatory power similar to using a low-yielding tester.

Quantitative genetics has undoubtedly contributed substantially to maize breeding methodology. Dr. Hallauer and J. B. Miranda, Filho have done an excellent job of summarizing quantitative genetics in maize in their book entitled *Quantitative Genetics and Maize Breeding*. The book is an extensive summary of quantitative genetic studies in maize and relates this information to the various breeding methods used in maize. The book is in the second edition and is in high demand by breeders throughout the world.

BREEDING METHODOLOGY

Dr. Hallauer's contributions to breeding methodology were influenced in part by the debate in the 1940s and 1950s over the importance of dominance and overdominance in the expression of heterosis for grain yield. Comstock et al. (1949) proposed half-sib reciprocal recurrent selection in response to this debate because this breeding method took advantage of all types of gene effects (including epistasis) and was only slightly less efficient than other methods when overdominance and/or epistasis were not important. Cockerham (1961) evaluated the expected genetic variance among unrelated single, three-way, and double crosses and demonstrated that the genetic variance among single crosses was always greater than among three-way crosses and that the genetic variance among three-way crosses was always greater than among double crosses. If only additive effects are important, then selection among single crosses would be twice as effective as selection among double crosses, and if nonadditive effects (dominance and epistasis) are important, selection among single crosses would be four times as effective as selection among double crosses. These theoretical developments and other concurrent developments paved the way for Dr. Hallauer's ideas on breeding methodology for developing superior maize single crosses.

Hallauer (1967a; 1967b) proposed a procedure for developing single-cross hybrids that maximized selection for nonadditive effects. The procedure required the use of two-eared maize populations. In the first phase, crosses are made between individual S_0 plants from two populations. At the same time the crosses are made, the S_0 plants are also selfed. In this way, both hybrids and S_1 lines could be developed from the same plants. The following year, the $S_0 \times S_0$ hybrids are evaluated in yield trials and the pairs of S_1 lines are grown in the nursery for further crossing and selfing. Dr. Hallauer recommended that four to six crosses be produced within each pair of S_1 lines. The procedure is then repeated until pure-line hybrids are developed. At each stage of evaluation, only the best hybrids are retained. In a comparison of $S_0 \times S_0$ crosses with the $S_1 \times S_1$ crosses, Dr. Hallauer showed that the first generation of selection was effective for improving grain yield. Hallauer (1967b) also outlined a procedure where one-eared source populations could be used.

Hallauer and Eberhart (1970) suggested a modification of the two-eared method for developing single crosses for population improvement. They called this method reciprocal full-sib selection to distinguish it from the reciprocal recurrent selection proposed by Comstock et al.

(1949). The method was to cross pairs of S_0 plants (one plant from each of two populations) and simultaneously self the plants. The $S_0 \times S_0$ hybrids are evaluated in yield trials, the best are selected, and remnant S_1 seed is used to intermate to form the two improved populations for continued selection. This breeding procedure incorporated yield testing of $S_0 \times S_0$ hybrids for population improvement as well as early testing of single-cross combinations. Thus, the best selections are used to form a new population for further selection and they are incorporated directly into a single-cross development program. One of the main advantages over reciprocal recurrent selection is that twice as many plants from the source populations can be evaluated using the same amount of resources required in reciprocal recurrent selection.

GERMPLASM DEVELOPMENT AND IMPROVEMENT

Much of Dr. Hallauer's efforts have been devoted to germplasm development and population improvement via recurrent selection. Dr. Hallauer works with both adapted temperate and exotic germplasm. He currently has 10 active recurrent selection programs involving 12 populations. The primary traits under selection are grain yield, grain moisture, root lodging, and stalk lodging. Other traits under selection in specific programs are ear length, maturity, and resistance to European corn borer (*Ostrinia nubilalis* Hübner). Once populations reach a desired level of performance, the improved populations are released to the general public and registered in *Crop Science.*

The progenies selected to form each new cycle of a population are routinely placed in a pedigree breeding program to assess their potential as parents of hybrids. This feature has been a hallmark of the Cooperative Federal-State Breeding Program that has resulted in the release of many influential inbred lines. Currently and traditionally, the responsibility for managing the pedigree breeding program has been with the state breeder. Dr. Hallauer currently has this responsibility, replacing Dr. W. A. Russell who retired in 1989. Inbred lines resulting from this program are released as parental lines to be used in public and private breeding programs. Although some may view this as competition with the private sector, that is not the intent and is one of the reasons that hybrid recommendations are never made. The development and release of parental lines is a natural extension of recurrent selection and is a way of transferring improved germplasm to the general public. The pedigree breeding program is also an invaluable aid in educating and training graduate students and monitoring progress in recurrent selection programs. It is noteworthy to point out that commercial germplasm has never been incorporated into any of the populations or inbred lines that have been released.

Dr. Hallauer has had great success in using recurrent selection to incorporate exotic germplasm into his breeding program. In his first work with tropical germplasm, Dr. Hallauer compared two methods of adapting "Eto Composite," a tropical maize population from Colombia, South America, to temperate climates. In the first method, he used mass selection for earlier silking and adaptation. In the second method, he crossed "Eto Composite" with six early inbred lines and intermated the resulting F_1's to form a new synthetic. He demonstrated that mass selection for adaptation and earlier silking was an effective method for adapting exotic germplasm to temperate environments. In the "Eto Composite," time to silking was decreased an average of four days per year with mass selection and required only five years to adapt "Eto Composite" to Iowa. This was an important finding because it allows the utilization of populations with 100% exotic germplasm, which increases the probability that novel genotypes will be derived from the population. The second method Dr. Hallauer used to adapt "Eto Composite" to Iowa involved the incorporation of corn-belt germplasm into the exotic germplasm, which raises issues about genetic recombination between the adapted and exotic genomes. Dr. Hallauer's research demonstrated that corn-belt germplasm does not need to be incorporated into tropical germplasm in order to adapt it to temperate environments.

By using the mass-selection technique, Dr. Hallauer has successfully adapted "Eto Composite," "Tuxpeño" (tropical germplasm obtained from CIMMYT in Mexico), "Antigua" (tropical germplasm obtained from CIMMYT in Mexico), and "Suwan-1" (tropical maize population developed in Thailand). Recurrent selection is ongoing in all of these populations except for "Antigua." Dr. Hallauer is currently adapting "Tusón" (tropical germplasm from the Caribbean and South America) and is converting adapted versions of "Mexican Dent" and "Cateto" (tropical germplasm from South America) × "Caribbean Flint" from white to yellow kernels. These populations have all been used extensively in their native environments. The adapted versions of these populations exhibit excellent yield potential and a greater incidence of disease and insect resistance than most corn-belt populations.

Dr. Hallauer has been involved with and participated in the release of many populations, synthetics, and inbred lines. He has been unselfish with his germplasm and is committed to the free exchange of germplasm. The dedication and commitment of Dr. Hallauer and other members of the Cooperative Federal-State Maize Breeding project in Ames to the free exchange of germplasm has made Ames one of the top centers in the world for the development and dissemination of maize germplasm.

GRADUATE EDUCATION

Dr. Hallauer is dedicated to graduate education. In 1966, he created a special topics course on quantitative genetics, which in 1969 was incorporated into the Department of Statistics where it has been taught ever since. He conducted a spring semester plant breeding seminar from 1975 to 1993, has taught advanced plant breeding since 1986, and taught field plot techniques in plant breeding from 1989 to 1994.

Dr. Hallauer has devoted much of his time to the training of graduate students. His students have come from the United States and 18 foreign countries. He has been major advisor to 75 students (51 Ph.D. and 24 M.S.) and has hosted 25 visiting scientists or postdoctoral students from 11 different countries. At Iowa State, he has served on more than 100 graduate student program of study committees. A host of domestic and foreign visitors have visited Dr. Hallauer and the maize breeding project.

HONORS AND AWARDS

Dr. Hallauer has been extensively recognized for his achievements and contributions to plant breeding and science. Within the state of Iowa, he received the Applied Research and Extension Award (ISU, 1981), the Distinguished Fellow Award (Iowa Academy of Sciences, 1995), a Faculty Citation Award (Iowa State Alumni Association, 1987), the Distinguished Service to Agriculture Award (Gamma Sigma Delta, ISU, 1990), a Governor's Science Award (Terry Branstad, Governor of Iowa, 1990), the C. F. Curtiss Distinguished Professor in Agriculture Award (ISU, 1991), the Burlington Northern Career Achievement in Research Award (ISU Foundation, 1991), the Henry A. Wallace Award for Distinguished Service to Agriculture (ISU Alumni Association, 1992), and a Distinguished Achievement Citation (ISU Alumni Association, 1995); he was elected an honorary member of the Iowa Crop Improvement Association (1995).

At the national level, Dr. Hallauer has been a member of the American Society of Agronomy (ASA) since 1958 and the Crops Science Society of America (CSSA) since 1961. He has served these societies in many ways and was elected a fellow of ASA (1979) and a fellow of CSSA (1985). He received the Crop Science Award (CSSA, 1981), the Agronomic Achievement Award—Crops (ASA, 1989), the Dekalb Crop Science Distinguished Career Award (CSSA, 1990), and the Agronomic Research Award (ASA, 1992). The commercial sector has recognized his achievements by awarding him the Northrup-King Recognition Award for Research in Corn Breeding (1984), the National Council of Commercial Plant Breeder's Genetics and Breeding Award (1984), and the National Agri-Marketing Association's Excellence in Research Award (1993). For his outstanding service to the USDA-ARS, Dr. Hallauer received the Scientist of the Year Award (1985) and was elected to the USDA-ARS Science Hall of Fame (1992). His crowning achievement, and one that has been attained by only a few maize breeders, was his election to the U.S. National Academy of Sciences.

THE MAN

Dr. Hallauer is a self-effacing man. Despite his achievements and recognition, he has remained humble and modest. He treats everyone as an equal and is always willing to listen, share his knowledge and germplasm, and help out in what ever way he can. He is a prolific writer, an outstanding editor, an avid reader, and an excellent speaker. For enjoyment, he reads books on history, including science history and U.S. and world history, and popular fiction. He has a great sense of humor and has that rare ability to incorporate humor into his seminars. He is a people person and makes friends easily. Arnel Hallauer is a man who has the distinction of being respected, admired, and loved by all.

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